

*About the binomen *Cylindropuntia rosea* (Cactaceae) and its invasive individuals recorded in the Valencian Community (Spain)*

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RESUMEN: El nombre *Cylindropuntia rosea* (DC.) Backeb., usualmente utilizado para designar el cactus invasor ‘Cardenche’ en la Comunidad Valenciana (España) es un binomen mal aplicado en muchos trabajos y que resulta ser un sinónimo heterotípico de *C. imbricata* (Haw.) F.M.Knuth, otra especie invasora también presente en este territorio. Bajo esta combinación se han indicado plantas que realmente corresponden a *C. pallida* (Rose) F.M. Knuth. La especie proviene de México, pero su origen filogenético es incierto, y pueden proponerse varias hipótesis para ello: que sea una verdadera especie, un híbrido alotetraploide *Cylindropuntia imbricata* × *tunicata* (Baker & al., 2009, *Haseltonia* 15: 117-134), o quizá tanto diploide como tetraploide para la misma combinación genética.

Palabras clave: *Cylindropuntia rosea*, *Cylindropuntia pallida*, *Cylindropuntia imbricata* × *tunicata*, Especies invasoras, Cactáceas.

ABSTRACT: *Cylindropuntia rosea* (DC.) Backeb., a name often used to designate the ‘Cardenche’ invasive cactus in the Valencian Community (Spain) is a misapplied binomen in many botanical works. The plants referred under this combination really match *C. imbricata* (Haw.) F.M.Knuth, another invasive species also found in this area. The plants referred under this name really match *C. pallida* (Rose) F.M. Knuth. This species is native from Mexico, but its phylogenetic origin is uncertain, and several hypothesis can be proposed: a true species, an allotetraploid hybrid *Cylindropuntia imbricata* × *tunicata* (Baker & al., 2009, *Haseltonia* 15: 117-134), and maybe both diploid and tetraploid allopolyploids from the same genetic combination.

Key words: *Cylindropuntia rosea*, *Cylindropuntia pallida*, *Cylindropuntia imbricata* × *tunicata*, Invasive species, Cacti, Polyploids

INTRODUCTION

The genus *Cylindropuntia* (Cactaceae) was proposed by Frederik Marcus Knuth in 1930 (Backeberg & Knuth, 1930). Six years later, an expanded second edition was published (Backeberg & Knuth, 1936) with a description of most of the species currently known. Nowadays, the correct name of the genus is *Cylindropuntia* (Engelm.) FM Knuth, Nye Kaktusbog: 102 (1930). FM Knuth (Backeberg & Knuth, 1936) proposed *O. imbricata* (Haw.) DC. as type species of the genus. Later on Backeberg (1942) propose *O. kleiniae* DC. but not

of them met the criteria of the International Code of Nomenclature (v. McNeill, 2012). Therefore in 2001, Doweld (2001: 22) edited the initial proposal of Backeberg, designating *O. arbuscula* Engelm. as the type species of the genus.

Knuth's proposal to create the genus *Cylindropuntia* grouped the cylindrical stems species of the genus *Opuntia* Mill. Therefore, he raised the subgenus proposed by Georg Engelmann (Engelmann, 1856) to the rank of genus (*Proc. Amer. Acad. Arts* 3: 302 (1856)). Subsequently, Curt Backeberg separated from this genus the thorny species without pods concentrated in South

Fig. 1. Appearance of individuals of *Cylindropuntia* invading the 'Sierra de Orihuela', Alicante, España.



Fig. 2. Flowering of an individual grown from the invader *Cylindropuntia* from 'La Sierra de Orihuela'.



America, creating a new genus: *Austrocylindropuntia* (Backeberg, 1938). Nowadays, the correct name of that genus is *Austrocylindropuntia* Backeb. in *Blatt. Kakteenf.* 1938 (6): [21] (1938). Although the protocol indicates in brackets (the pages were not numbered) the page 21, this page corresponds to the description in English. In the page 19, it appears also in German language. Finally, from this separation of genus, the genuine *Cylindropuntia* was the old *Opuntia* with cylindrical stems and spines with pods, typical of Middle and North America.

In the eastern part of the Iberian Peninsula several species of *Austrocylindropuntia* and *Cylindropuntia* were used as crops. Some of those species were recorded as naturalized or invasive. Guillot & al. (2008) explained this situation in Comunidad Valenciana, Spain. The most common invasive taxon is *A. subulata* (Muehlenpf.) Backeb. [= *C. subulata* (Muehlenpf.) P.M. Knuth; = *O. subulata* (Muehlenpf.) Engelm.]. It is very common in the vicinity of residential areas, especially near the coast. Within *Cylindropuntia* genus, different species can be distinguished by their grow form (tree or shrub), thickness of cladodes (<3cm or >3cm), and colour and density of the thorns and the floral tepals. The thorns can be distinguished between those plants that possess highly clustered, radially and greater length between the areola (knuckles parenchyma hardly visible), and those which either have just few spines or at least because of their colour, size..., the parenchyma is more visible. The first group are easy to appreciate in the landscape because of their silver or ivory appearance, intricate and heavily armed. The second group typically exhibits a less aggressive appearance. Within the first group of plants, a kind of (1-1.2 m), with skin colour flowers and sterile fruits was located in the 80s in the south of Alicante (Valencia, Spain) (figs. 1-2). At the beginning it was recorded by one of the authors of this work as *Cylindropuntia tunicata* (Lehm.) F.M. Knuth [= *O. tunicata* (Lehm.) Pfeiff.] [Alicante: 30SXH7918 and 8018, Orihuela, Monte de Orihuela pr. St. Anton, 7-II-1987, E. Laguna]. As explained above, this identification was incorrect. Although *C. tunicata* was also found later in some areas of Valencia (Guillot & al., 2008; Mateo & al., 2013).

The finding of the Orihuela individual as well as another subsequent recordings, constitute the first reference of *O. tunicata* in the plant identification keys of Valencia (Mateo & Crespo, 2001). The term *O. tunica* was used between 1900 and 2000s during the early eradication plans of this species in Valencia (Orihuela, Liria, Benidorm...).

But from 2004 (Sanz & al., 2004: 138-139) until now, this same species is being called *Cylindropuntia rosea* (DC.), with 'Cardenche' as common name, and is the target of several intensive eradication programs (Deltoro & al., 2011).

Over recent years, thanks of contact with specialists from other countries we detected disagreements on the correct name and synonyms for the species found in Orihuela (short length, compact shape, pink-skin colour flowers and abundance of ivory thorns which do not allow distinguishing the parenchyma on the knuckles).

The term *C. rosea* is being used in Australia and Mexico (see below), while *C. pallida* (Rose) F. M. Knuth is being used in North America and South Africa (see Weed Research Programme, 2012: 4; Walters & al., 2011: 129). In South Africa this species has also been previously confused not only with *C. tunicata* but with *C. fulgida* (Engelm.) F.M. Knuth (Henderson & Zimmermann, 2003). The main reason of this confusion is the similarity between the seedlings of those three species (Walters & al., 2011). In this paper we analysed the origin of this problem, recommending the exclusive use of one of them. We also studied the relation of those three names with the invasive species *C. imbricata* (Haw.) F.M. Knuth, and its potential hybrids.

Opuntia pallida vs. *Opuntia rosea*

During the last years in Spain the plant found in Orihuela (no tree-like, pink flowers) was referred as *Cylindropuntia rosea* (DC.) Backeb., *Cactaceae* (Backeberg) 1: 197 (1958) [= *Opuntia rosea* DC., Prodr. 3: 471 (1828), Basión.; = *Grusonia rosea* (DC.) G.D. Rowley in *Tephrocactus* Study Group 12(3): 45 (2006)]. See Sanz & al. (2004), Guillot & al. (2008) or Sanz & al. (2011). Backeberg (1958) recombined into *Cylindropuntia* the *O. rosea* described by De Candolle in 1828 (from Tula, State of Hidalgo, Mexico) (figs. 3, 4), including among its synonyms *C. pallida* (Rose) F.M. Knuth in Backeb. & Knuth, *Kaktus-ABC*: 126 (1936) [= *O. pallida* Rose in *Smithsonian Misc. Collect.* 50: 507 (1908), Basión.].

The description of *C. rosea* (Backeberg, 1958: 200 y 201) can be considered as a translation of the description of *Opuntia pallida* made in 1908 by Rose (see Britton & Rose, 1919: 66). It is obvious that Backeberg considered that *O. rosea* (De Candolle, 1928) was the same species as *O. pallida* (Rose, 1908; Britton & Rose, 1919) (figs. 5-6).

Fig. 3. Original description of *Opuntia rosea* DC. in 'Prodromus' (De Candolle, 1828a). Accessed for non-commercial use at Botanicus [<http://www.botanicus.org>] and Biodiversity Heritage Library, [<http://www.biodiversitylibrary.org/>].

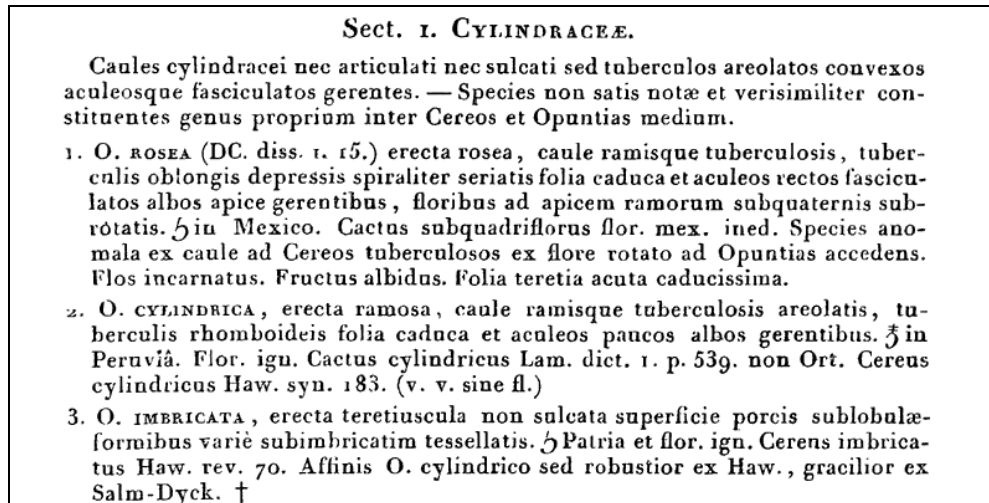


Fig. 4. Description of *Opuntia rosea* in 'Revue des Cactées' De Candolle (1828b, 1829). Accessed for non-commercial use at Botanicus [<http://www.botanicus.org>] and Biodiversity Heritage Library, [<http://www.biodiversitylibrary.org/>].

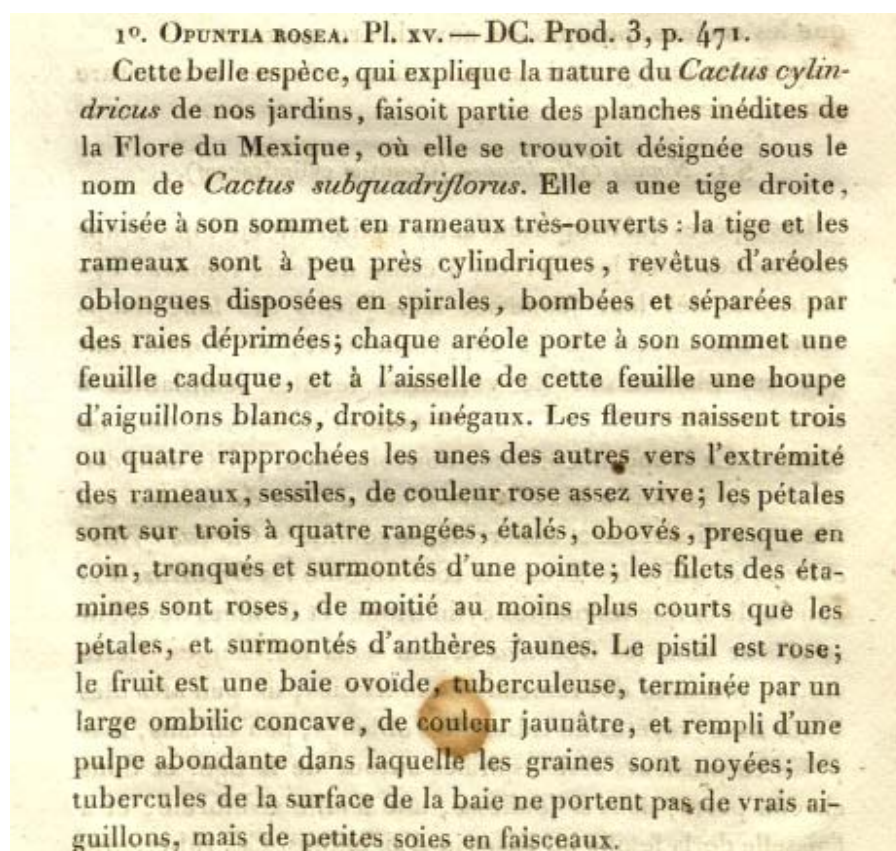


Fig. 5. Description of *Opuntia pallida* by Rose (1908). Accessed for non-commercial use at Botanicus [<http://www.botanicus.org>] and Biodiversity Heritage Library, [<http://www.biodiversitylibrary.org/>].

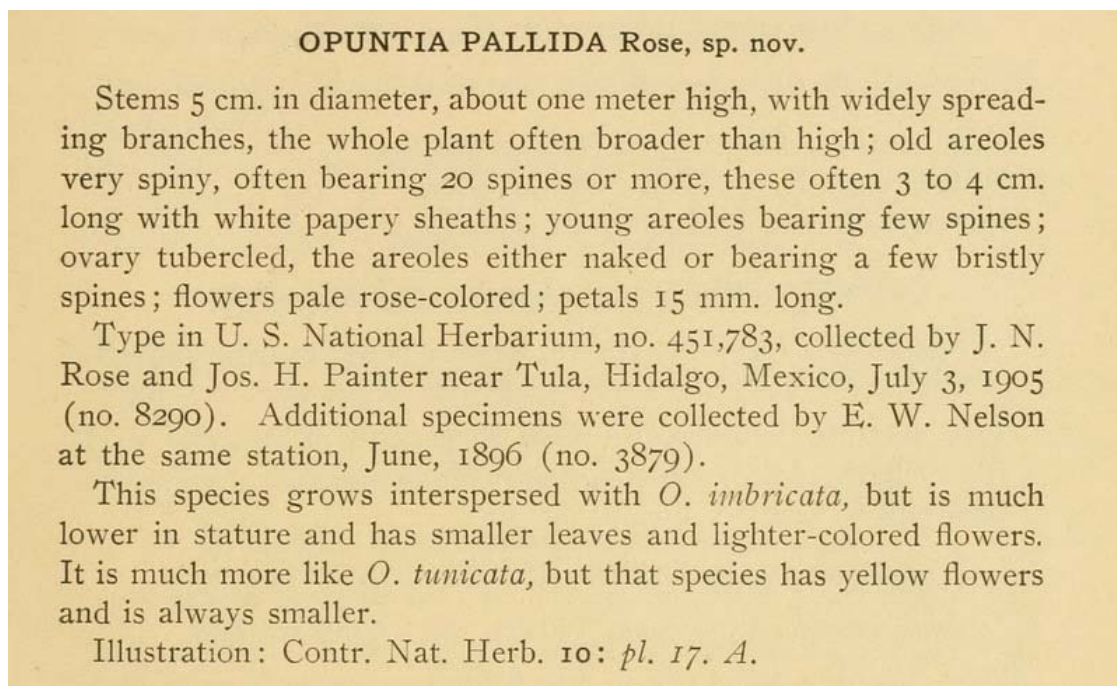
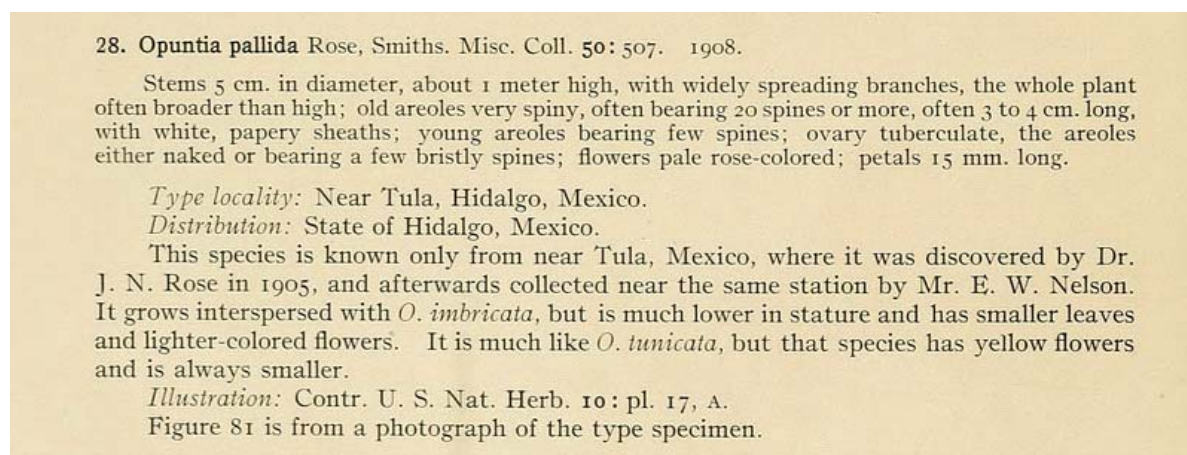


Fig. 6. *Opuntia pallida* by Britton & Rose (1919). Accessed for non-commercial use at Botanicus [<http://www.botanicus.org>] and Biodiversity Heritage Library, [<http://www.biodiversitylibrary.org/>].



The description of *Opuntia pallida* (Rose, 1908; Britton & Rose, 1919) fit with the characteristics present by the species recorded as *C. rosea* naturalized in Comunidad Valenciana. As Britton & Rose (1919: 66) confirmed, this plant was illustrated in 1906 (Rose, 1906: 65) and referred as *O. tunicata* (Lehm.) Link & Otto [= *Cylindropuntia tunicata* (Lehm.) F.M. Knuth]; morphologically similar but smaller and with yellow tepals. The individual from which the sample for the *typus* of the species was taken in 1905 by Rose nearby Tula was illustrated by Britton & Rose (1919: 65, fig. 81). Overall, it is clear that the reference to Tula as native location for *C. rosea* (Backeberg, 1958: 198) was extracted from the description of *O. pallida* (Rose, 1908 : 507; Britton & Rose, 1919 : 66 , item 28).

Considering the current rules of the International Code of Nomenclature for algae, fungi and plants or Code of Melbourne (McNeill, 2012), as *O. rosea* DC. was described before *C. rosea* (DC.) Backeb. and they are synonyms (Bravo-Hollis, 1978; Anderson, 2001: 212), *O. rosea* DC. should be the used term. In fact, most of the Mexican (Guz-

mán & *al.*, 2003; Arias & *al.*, 1997) and Australian (AWC, 2011; Chah 2005; Ewa, 2011; Holtkamp, 2006; Hosking, 2004; Johnson & *al.*, 2009) authors were using the term *O. rosea*. In all cases, the term used for the plant from ‘La Sierra de Orihuela’, Valencia, is *C. rosea* instead of *C. pallida*, giving the latter term as a synonym of the first one.

Identity of *Opuntia rosea* DC.: *O. rosea* vs. *O. imbricata*.

The previous equivalence contradicts the description of Britton & Rose (1919). They said that *Opuntia rosea* DC. is a synonym of *Opuntia imbricata* (Haw.) DC. (figs. 7-8). *O. imbricata* is a widespread horticultural cacti species since the eighteenth century. Nowadays its correct name is *Cylindropuntia imbricata* (Haw.) F.M.Knuth in Backeb. & Knuth, *Kaktus-ABC*: 125 (1936) [= *Cereus imbricatus* Haw., *Revis. Pl. Succ.*: 70 (1821) Basión.; ≡ *O. imbricata* (Haw.) DC., *Prodr.* 3: 471 (1828)]. Its original description was often erroneously cited as Haworth (1819) instead of Haworth (1821) (fig. 9).

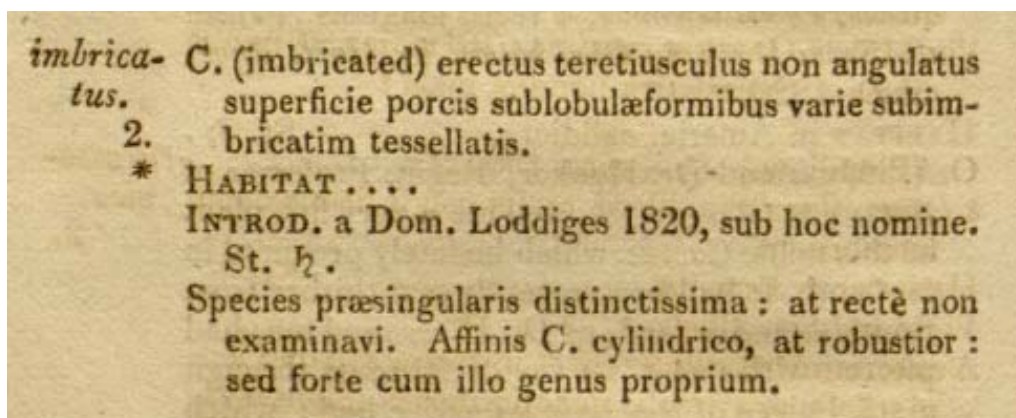
Fig. 7. Flowers and stems of *Cylindropuntia imbricata* in Llíria, Valencia, Spain.



Fig. 8. Morfology of of *Cylindropuntia imbricata* in Lliria, Valencia, Spain.



Fig. 9. Description of *Cereus imbricatus* by Haworth (1821). Accessed for non-commercial use at Botanicus [<http://www.botanicus.org>] and Biodiversity Heritage Library, [<http://www.biodiversitylibrary.org/>].



The original description of *Opuntia rosea* (De Candolle, 1828a) is particularly brief, although it includes details that do not match those of the invasive plant that we consider as *Cylindropuntia rosea*: upright growth, presence of erect carriage, or presence of aculeus with white tips (instead of the whole thorn white). The author also indicates white fruits and cylindrical fleshy lose leafs. All these characters are not typical characters of the invasive

plant here discussed, but of *C. imbricata*. De Candolle cited *Cactus subquadriflorus* of the '*Flora Mexicana*' as the reference for *O. rosea* (see González Bueno & Rodríguez Nozal, 2006), although the original publication was *Cactus quadriflorus* (McVaughan, 2000). McVaughan considers that the original sheet of *Flora Mexicana* is well reproduced in '*Revue des Cactées*' (De Candolle, 1828; 1829) (fig. 11).

'*Flora Mexicana*' had a print edition published by the Mexican government (Sessé & Mocino, 1894), without any description of *Cactus subquadriflorus* or *C. quadriflorus*. Nowadays *Cactus subquadriflorus* from '*Flora Mexicana*' is often cited as *Cactus subquadriflorus* Mocino & Sessé ex DC., *Prodr.* 3: 471 (1828). Although Britton & Rose (1923: 254) were not sure of the equivalence between *C. subquadriflorus* and *Opuntia imbricata* Haw. (Britton & Rose, 1919), the description of De Candolle corresponds to *Opuntia imbricata* Haw. (Rowley, 1994). The twisty ends of the branches, the color of the leaves, the position of the thorns or the white color of the ripe fruit of the plant are clear characters of *C. imbricata*, not present in *C. pallida*.

Candolle (1828a) consulted the description of *Cereus imbricatus* (Haworth, 1819: 70) and recombined it as *Opuntia* without checking live or dead material. Subsequently he doubt that it can fit into '*Opuntiae cylindraceae*' (De Candolle, 1928b and 1929: 66) (fig. 10) and he recorded it as *Opuntia rosea* and *O. cylindrica* (Lam.) DC., [= *Austrocylindropuntia cylindrica* (Lam.) Backeb.]. Interestingly, De Candolle considered that the plant he was describing as *O. rosea* was different from the one that Haworth described before.

Overall, the correct terms for those species are:

Cylindropuntia pallida (Rose) F.M. Knuth in *Backeb. & Knuth, Kaktus-ABC*: 126 (1936)

≡ *Opuntia pallida* Rose in *Smithsonian Misc. Collect.* 50: 507 (1908) [Basi6n.]

- *O. rosea* auct., non DC.; - *C. rosea* auct., non (DC.) Backeb.: Sanz & al. in *Atlas de las Plantas Al6ctonas Invasoras de Espa6a* (2004: 138-139); Guillot & al. in *Flora Al6ctona Valenciana: La familia Cactaceae* (2008: 29)

Cylindropuntia imbricata (Haw.) F.M. Knuth in *Backeb. & Knuth, Kaktus-ABC*: 125 (1936)

≡ *Cereus imbricatus* Haw., *Revis. Pl. Succ.*: 70 (1821) [Basi6n.]

≡ *O. imbricata* (Haw.) DC., *Prodr.* 3: 471 (1828).

= *Cylindropuntia rosea* (DC.) Backeb., *Die Cactaceae* (Backeberg) 1: 197 (1958) [= *Opuntia rosea* DC., *Prodr.* 3: 471 (1828), Basi6n.; ≡ *Grusonia rosea* (DC.) G.D. Rowley in *Tephrocactus Study Group* 12(3): 45 (2006)].

The difference between those species has also a chromosomal fundament (Marc A. Baker, personal communication):

C. imbricata: n=11, 2n=2x=22 (Pinkava, 1999;

Baker & al., 2009a)

C. pallida: n=22, 2n=4x=44 (Baker & al., 2009b).

Fig. 10. Beginning of page 66 of '*Revue des Cact6es*' (1828-1829), referring the section *Cylindraceae* DC. of *Opuntia* Mill. It indicates that *Opuntia imbricata* (Haw.) DC. cannot be included in the group as it was stated in '*Prodromus*' few month before. Accessed for non-commercial use at Botanicus [<http://www.botanicus.org>] and Biodiversity Heritage Library, [<http://www.biodiversitylibrary.org/>].

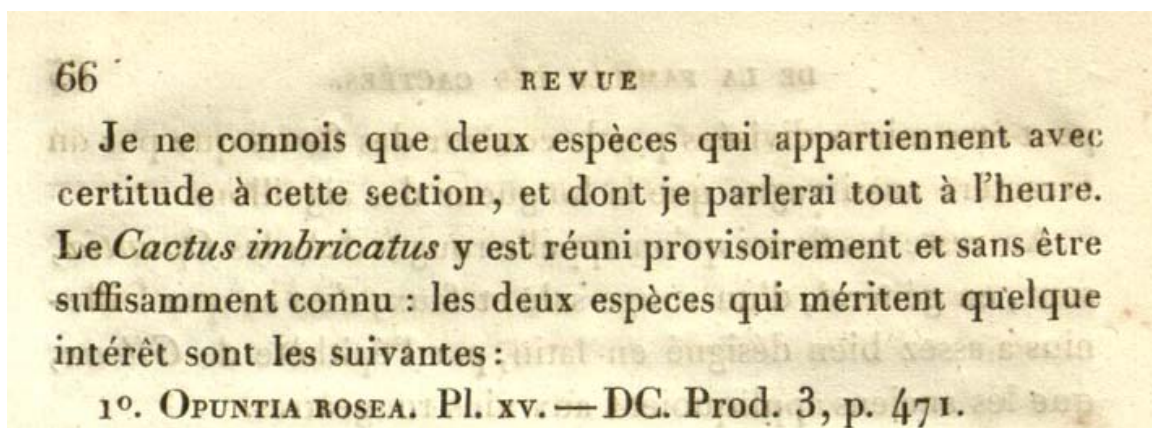


Fig. 11. *Opuntia rosea* in 'Revue des Cactées', De Candolle (1828b, 1829). Replica of 'Flora Mexicana' (Mc-Vaughan, 2000). Accessed for non-commercial use at Botanicus [<http://www.botanicus.org>] and Biodiversity Heritage Library, [<http://www.biodiversitylibrary.org/>].



Origin of *C. pallida*

There are several hypotheses about the origin of *C. pallida*. It seems that the plants recorded in Spain, South Africa or Australia are homogeneous since they would have their origin in the same clones introduced vegetatively. But in the native range, Mexico, there could be a great variability between regions. Even diploid and tetraploid individuals could be recorded with the same name.

Cylindropuntia pallida as genuine species

The initial hypothesis was that *C. pallida* was a genuine species. The tetraploid type indicated by Baker & al. (2009b) is not inconsistent with it. Neither if this tetraploid type would be a mutation derived from *C. tunicata* or a common ancestor with that species, without intervention of *C. imbricata* in the gene pool. Considering the distribution data provided by Guzman & al. (2003), (here cited as *C. rosea*) it could be an endemism of the Mexican states of Hidalgo, Mexico, Puebla and Tlaxcala. *C. pallida* is morphologically close to *C. tunicata*, except for the floral colour (skin colour instead of intense yellow) and height (higher). Genetic comparisons in *Opuntioideae* (Griffith & Porter (2009)) would include *C. pallida* (there indicated as *C. rosea*) within *C. tunicata* (211, clado B). Similarly, in its chromosome counts of *C. tunicata*, Baker (personal communication) found a tetraploid individual ($2n = 4x = 44$). There are more hypotheses about the homogeneity of the taxon present in Australia, South Africa and Spain as for example the specificity of biotypes of the cochineal insect *Dactylopius tomentosus* (Mathenge & al., 2006). The specific cochineal of *C. pallida* does not develop in *C. imbricata* or *C. tunicata* and the opposite applies to the cochineal of *C. imbricata* (Walters & al. 2011). This high specificity indicates that a hybrid origin is unlikely. Also, several studies have suggested that *C. pallida* could be a hybrid combination between *Cylindropuntia imbricata* \times *tunicata*, although to our knowledge there is the risk that, because of the lack of molecular and chromosomal studies, there are several groups that should be considered as different taxa.

Cylindropuntia \times *pallida*, allotetraploid *Cylindropuntia imbricata* \times *tunicata*

Baker & al. (2009b) considers that *C. pallida* could have its origin in an allopolyploid hybrid between *C. imbricata* ($2n=22$) and *C. tunicata* ($2n=22$). The chromosome determination ($2n = 4x = 44$) was made on material from Tula, but the authors

suggest that where both parents live sometimes it is possible to observe intermediate forms.

The allotetraploidy hypothesis clashes with some issues of reproductive biology: it is not predictable that from the combination of two diploid species it regularly appears a tetraploid hybrid. It could happen from the union of two anomalous gametes without meiosis Comai (2005), but it is unlikely. Regardless its origin, if the tetraploidy hypothesis is applied to the previously cited Mexican states, it could be a plant of ancient origin that would have been propagated vegetatively because of its characteristics. Also, the tetraploid could hybridize again, although these new hybrids should be sterile (triploidy). However, taking into account the relative variability of *C. tunicata* and *C. imbricata* (Bravo-Hollis, 1978; Benson, 1982; Anderson, 2001; Pinkava, 2003; Powell & Weedin, 2004), if their origin is in allotetraploidy there could be new morphotypes in different areas.

It should be noted that against Baker & al. (2009b), the use of hybrid notation (\times) is usually reserved for the 'alive hybrids', which are generated *in situ*. This would be difficult to apply in this case since we are talking about an allopolyploidy propagated vegetatively. In independent cases like this in the European flora (such as *Asplenium majoricum* Litard.) it is considered a taxon originated in ancient times that can propagate independently of their parents.

Cylindropuntia \times *pallida*, allopolyploidy *Cylindropuntia imbricata* \times *tunicata*

An alternative approach is the diploid hybrids *Cylindropuntia imbricata* \times *tunicata*, one of which in the past could generate the tetraploids of *C. pallida*. This diploid could be more widespread than the typical tetraploid, since both parents are overlapped from the South of the U.S. to South-central Mexico. In fact, there are hybrids with different morphological gradations beyond the 4 aforementioned Mexican states, recorded as *Cylindropuntia imbricata* \times *tunicata*, *C. \times pallida* or *Opuntia* \times *pallida*. There are few references, but they have been recorded through different states of N and central Mexico.

The website of Intermountain Herbaria (<http://intermountainbiota.org/portal/index.php>) collects several references from Dr. Marc A. Baker, recording *Cylindropuntia imbricata* \times *tunicata* individuals further north than the traditionally area of distribution of *C. pallida*. They reflect the existence of several degrees of introgression or backcrossing. They could have their origin in a combination between haploid hybrids or between tetraploid *C.*

pallida and its parents. Scheinvar (2004) recorded this plant in the Mexican state of Querétaro as *C. imbricata* \times *tunicata*, and provides an illustration.

The term *Cylindropuntia* \times *pallida* was already used in several publications before (Tejero-Díaz & Castilla Hernández (1999: 46); Calderón & Rzedowski (2001: 467)). But there are not chromosomal measurements link to those publications. Moreover, beyond the area originally recorded as native to *C. pallida*, there are not references of intermediate characters (as orange flowers). This fact could play against the hypothesis of the hybrid generated *in situ* and *inter diploid parents*.

CONCLUSIONS

-The priority name for the species recorded as *C. rosea* in Spain and Australia is *C. pallida*. *C. rosea* should be considered as a synonym of *C. imbricata*.

-There are several hypotheses to explain the origin of *C. pallida*, from genuine species to a hybrid origin. The only material analysed so far (from Tula, Hidalgo, Mexico) has been recorded as the allotetraploid *C. imbricata* \times *tunicata* and has been called *C* \times *pallida*.

-From this review we consider that the diploid hybrid *C. imbricata* \times *tunicata* could exist, which could justify the location of morphological transitions illustrated in some texts by Mexican authors.

Overall, we consider that there is a need to review all the alien populations (such as the aforementioned of Liria, Valencia, Spain) where there is a concurrence of *C. pallida*, *C. imbricata* and *C. tunicata* and analyse the chromosomal configuration in both adult plants and seedlings, as well as look for the existence of hybrids between them.

Acknowledgments: To Dr. Marc A. Baker (Southwest Botanical Research, Prescott College and Arizona State University) for all the information provided on chromosome studies and other biological aspects of *C. pallida*.

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(Recibido el 12-X-2013) (Aceptado el 25-X-2013).